A KINGFISHER (HALCYONIDAE) FROM THE MIOCENE OF RIVERSLEIGH, NORTHWESTERN QUEENSLAND, WITH COMMENTS ON THE EVOLUTION OF KINGFISHERS IN AUSTRALO-PAPUA

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A Miocene kingfisher from Riversleigh, northwestern Queensland, represented by a complete carpometacarpus, is the earliest record of the Halcyonidae from Australasia. It shares similarities with several modern genera, but a positive generic identification cannot be made. Although it can be distinguished from extant species, this skeletal element is insufficient to erect a new genus. A processus dentiformis in *Tanysiptera* and *Melidora* and its absence in *Todiramphus* and other genera suggest that the former genera are among the more primitive of the Australo-Papuan kingfishers. The less developed processus dentiformis in the Riversleigh specimen is consistent with it being an earlier member of the *Todiramphus* lineage. Of living kingfishers examined, all that retain the processus dentiformis are inhabitants of rainforest. □ *Kingfisher, Halcyonidae, Riversleigh, Miocene, evolution.*

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The kingfishers (Alcedinidae s.l.) are subdivided into 3 subfamilies. DNA-DNA hybridisation studies (Sibley & Ahlquist, 1990) suggested that these should be recognised as families. Cerylidae do not occur in Australasia. Alcedinidae ('river kingfishers') and Halcyonidae [= Daclonidae auct] ('tree kingfishers') are represented in Australo-Papua by 5 species in 1 genus and 21 species in 5-6 genera, respectively (Beehler et al., 1986; Fry et al., 1992; Christidis & Boles, 1994).

There are no named Tertiary forms from outside Australasia (Olson, 1985). Mourer-Chaurviré (1982) listed this family (Alcedinidae s.l.) from Eocene-Oligocene deposits at Quercy, France, and Olson (1985) noted that he had examined specimens close to this family originating from the lower Eocene of North America and the medial Eocene of Germany. All Australian Quaternary kingfisher material is referable to modern taxa: *Alcedo azurea, Dacelo novaeguineae, Todiramphus pyrrhopygia* and *To. sanctus* (Baird, 1991). No Tertiary kingfishers are known from Australasia (Fordyce, 1991; Vickers-Rich, 1991).

Described herein is a Miocene kingfisher from Riversleigh, northwestern Queensland.

METHODS

Measurements (Steadman, 1980) were made with vernier calipers accurate to 0.05mm and rounded to the nearest 0.1mm. Terminology of bones largely follows Baumel & Witmer (1993). *Todiramphus* and *Syma* are considered distinct from *Halcyon*, following Christidis & Boles (1994). Institutional prefixes are AM (Australian Museum), ANWC (Australian National Wildlife Collection), MV (Museum of Victoria), QM (Queensland Museum) and USNM (United States National Museum).

SYSTEMATIC PALAEONTOLOGY

Family HALCYONIDAE

Although the Halcyonidae includes some of the largest kingfishers in the world, size is not a valid character for family allocation of osteological material. Australia's 2 Alcedinidae, *Alcedo pusilla* and *A. azurea*, are the country's smallest kingfisher species (wing lengths 55mm and 75mm, respectively), but the closely related *A. websteri* of New Britain has a wing length of 90mm, overlapping in size the smaller halcyonids (e.g., *Todiramphus macleayii*, wing length 90mm).

The carpometacarpus of the Halcyonidae can be distinguished from that of the Alcedinidae and Cerylidae (Table 1) and on this basis the Riversleigh fossil is assigned to the Halcyonidae.

Halcyonid gen. indet.
Fig. 1C

MATERIAL. QMF29719, right carpometacarpus with only minor abrasion to some surfaces from ?middle

TABLE 1. Characters for separating the carpometacarpus of the Alcedinidae, Cerylidae and Halcyonidae.

Character	Alcedinidae	Cerylidae	Halcyonidae
proximal border of dorsal carpal trochlea	more angular	more rounded	more angular
development of os metacarpalis alulare	more gracile	more robust	more robust
orientation of os metacarpalis alulare	more caudal	more caudal	more proximal
tip of processus extensorius	rounded	expanded, slightly rugose	rounded
position of processus intermetacarpalis	more proximal	more proximal	more distal
width and distal extension of sulcus interosseus	narrower, not as extensive distad	broad, extending almost to facies digitalis minor	broad, extending almost to facies digitalis minor
plane of synostosis metacarpalis distalis and distal ends of os metacarpalis major and os metacarpalis minor	os metacarpalis minor depressed below plane	os metacarpalis minor depressed slightly below plane	flat, coplanar

Miocene to early late Miocene Last Minute Site from System C (Archer et al., 1989, 1994). This site is interpreted to represent shallow pools or even emergent accreting surfaces, and is dominated by terrestrial vertebrates including the possums *Djilgaringa gillespieae* Archer et al., 1987 and *Strigocuscus reidi* Flannery & Archer, 1987. Other avian taxa from this site are a range of passerines, including the logrunner *Orthonyx kaldowinyeri* Boles, 1993.

DESCRIPTION. Length 15.8mm. Length of spatium intermetacarpale 61% of length of carpometacarpus. Processus dentiformis low and pointed, located about midway between the distal edge of facies articularis alularis and the cranialmost point of facies articularis digitalis major. Os metacarpale majus of about equal thickness for entire length, in ventral view. Spatium intermetacarpale gradually becoming wider distally. Processus intermetacarpalis far proximally in spatium intermetacarpale.

REMARKS. Among extant Australo-Papuan Halcyonidae, *Tanysiptera* and *Melidora* have a low, flat processus dentiformis, *Syma* has an almost non-existent processus dentiformis as a barely raised roughened area, and *Todiramphus* and *Dacelo*, as well as Afro-Asian *Halcyon*, lack it (Boles unpubl. data). X-ray photographyof study skins showed *Actenoides* and *Lacedo* have a low processus dentiformis, but *Halcyon (Pelargopsis)* and *Clytoceyx* do not. The x-rays, while sufficient for determining this process, are not adequate for detailed comparisons of these taxa. Other than size, there are not substantive differences between the carpometacarpi of *Todiramphus*, *Dacelo* (and presumably *Clytoceyx*); *Syma* differs only in its low processus dentiformis. Because *Dacelo* and *Clytoceyx* are considerably larger (*D. novaeguineae* 32.5-35.6mm), they are not considered further. Subse-

quent comparisons involve *Todiramphus*, *Syma*, *Tanysiptera* and *Melidora*.

The fossil (length 15.8mm) is in the size range of *Tanysiptera* (*sylvia* 14.0-15.2mm; *galatea* 15.2-16.5mm) and *Todiramphus* (*sanctus* 14.8-15.1mm; *macleayii* 14.5-15.7mm; *pyrrhopygia* 15.7-16.5mm; *chloris* 16.5-17.8mm). It is larger than *Syma* (*torotoro* 13.5mm; *megarhyncha* 14.4mm) and smaller than *Melidora macrorrhina* (18.9 mm). It differs from *Tanysiptera* and *Melidora* and resembles *Syma* and *Todiramphus* by being more slender and by having spatium intermetacarpale longer relative to the length of carpometacarpus and the dorsal rim of trochlea carpalis extending less distally relative to the ventral rim. The fossil differs from *Todiramphus* and resembles *Tanysiptera*, *Melidora* and *Syma* by having processus dentiformis present. This process, however, is narrow and pointed, rather than broad and flat as in these genera (and larger than in *Syma*), and is situated more proximally relative to the spatium intermetacarpale and processus intermetacarpalis than in *Tanysiptera* and *Melidora*, and more distally than in *Syma*. From all 4 genera, the Riversleigh specimen differs by having the caudal edge of os metacarpale majus straighter and less caudally concave, making os metacarpale majus thicker and spatium intermetacarpale proportionally narrower relative to the width of the carpometacarpus.

The significance of these differences is uncertain. They are individually minor, yet within the Halcyonidae the amount of variation in this bone is little so that these differences may assume greater importance. Variation in the carpometacarpus, however, is not representative of that of the remainder of the skeleton or indeed the rest of the morphology (Boles unpubl. data).

The fossil cannot be assigned to *Tanysiptera*, *Melidora*, *Syma* or *Todiramphus* and can be differentiated from extant species of these genera.
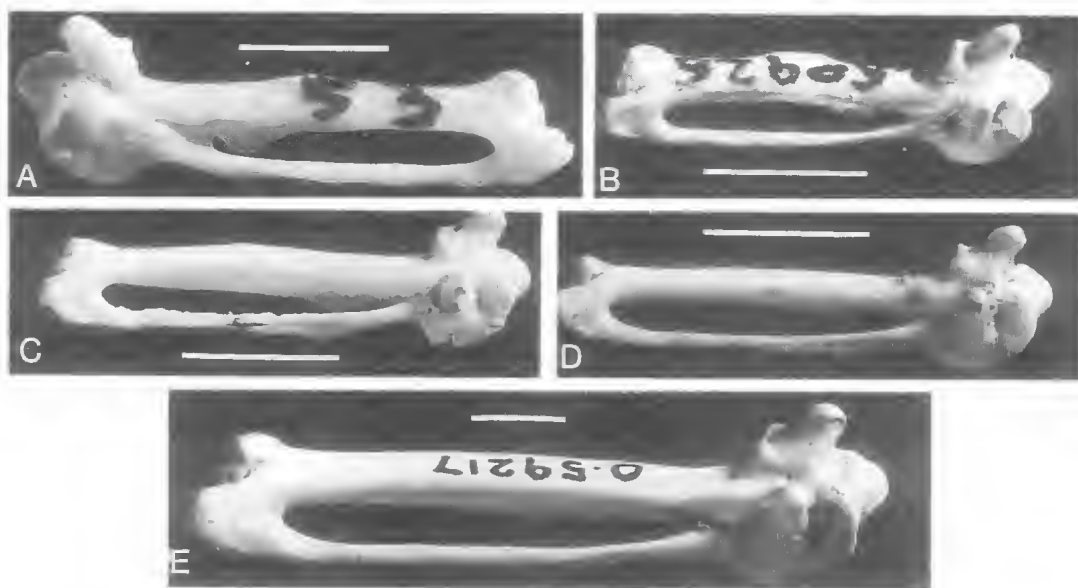
FIG. 1. Carpometacarpi of Australo-Papuan halcyonid kingfishers, in ventral view. All right side except for B. A, *Melidora macrorrhina* (ANWC CORS-53). B, *Tanysiptera sylvia* (AMO.60926). C, Riversleigh Halcyonidae gen. indet. (QMF29719). D, *Todiramphus sanctus* (AMO.57182). E, *Dacelo novaeguineae* (AM O.59217). Scales = 5mm.

Overall it has the greatest resemblance to species of *Todiramphus* in size and morphology, despite the presence of a small processus dentiformis. Given the relatively limited importance of carpometacarpal variation in the halcyonids and the limited fossil material it is imprudent to recognise a new genus at this time.

DISCUSSION

To place the Riversleigh fossil in perspective within halcyonid kingfisher evolution, the primitive members of the family must be identified. Fry (1980a, b) employed 3 criteria for this. Primitive kingfishers have 1) generalised diets and relatively unspecialised modes of foraging (i.e.: sitting and pouncing, non-fishing); 2, stable habitats and not of recent origin (rainforest), within which they may be discontinuously or relictually distributed; and 3, oligotypic genera (i.e. with few species) without close relatives. Fry (1980a) concluded that kingfishers (all families as recognised here) arose in Malesia, the area between Indo-China and the Coral Sea.

Prominent among the primitive forms were halcyonid kingfishers, many of which live in Malesian rainforests. Fry (1980a) speculated that 'the Daceloninae [= Halcyonidae] have a history of evolution in eastern equatorial rainforests al-

most as ancient as the mid-Cenozoic origin of the Alcediniformes [sensu Feduccia (1977)]'. By the early Miocene, the present geographical configuration of Malesia had been reached. This, in Fry's opinion, provided 'ideal circumstances for the multiplication of species, resulting in a fauna of forest-dwelling, non-fishing kingfishers ... At some more recent time, perhaps about the mid-Pliocene, this fauna gave rise to a lineage, *Halcyon* [s.l.], adapting to more open habitats'.

Under this suggested sequence of events, the rainforest-dwelling *Tanysiptera*, *Melidora*, *Actenoides* and *Lacedo* would be among the more primitive genera. *Todiramphus*, included by Fry (1980a) in his open habitat *Halcyon*, would be more derived. Presumably *Syma* (also included in *Halcyon* sensu Fry [1980a]) also was considered by Fry (1980a) to be a more derived taxon. Although entering open country adjacent to forest, the two species of *Syma* are essentially rainforest inhabitants, particularly in New Guinea (Coates, 1985).

In addition to sharing the primitive characters proposed by Fry (1980a, b), species of *Tanysiptera* and *Melidora* (as well as *Actenoides* and *Lacedo*) have a low but well-defined processus dentiformis on the carpometacarpus. This is absent in the other halcyonid genera examined, the Alcedinidae and Cerylidae, and some other cora-

ciiform families (e.g. Momotidae, Coraciidae). If any of these families is used for outgroup comparisons, the suggested polarity of the processus dentiformis is that its presence is derived. A similar comparison using other coraciiform families (Todidae, Phoeniculidae, Upupidae, Bucerotidae), in which the structure is present, gives the opposite conclusion: presence of the processus dentiformis is primitive, its absence derived. Within the Meropidae, the structure is present in some species (*Merops ornatus*) and absent in others (*M. apiaster*). The significance of this variation is unknown, as are the functional aspects of the processus dentiformis. Thus the polarity of this character's presence is not known. (This, of course, assumes that the processus dentiformis is homologous across the order. Whether this is so, and what relationship it has to the similar process found in the majority of the Passeriformes, is unknown.) Within the halcyonid kingfishers the presence of the processus dentiformis exhibits a strong correlation with Fry's (1980a,b) primitive criteria.

Superficially there seems to be little in common externally between *Melidora* and *Tanysiptera* beyond the basic kingfisher similarities. Each has specialised generic characters: a hooked bill in *Melidora* (Hooked-billed Kingfisher) and elongated, spatulate central rectrices in *Tanysiptera* (paradise kingfishers). *Melidora macrorrhina* is a rather drably coloured species. Other than blue scalloping on the crown, the plumage is a combination of browns and white. The underside is white, while the back, rump, tail, and wings are dark brown with paler brown scalloping. This plumage is quite unlike that of the paradise-kingfishers *Tanysiptera*, adults of which are strikingly patterned in unmarked blues and blacks, and usually either white or buff/rose. The juvenile plumage of *Tanysiptera*, however, is brown with scalloping, and Fry (1980b) was 'impressed by its [*Melidora*'s] plumage resemblance to the distinctive juvenile of *Tanysiptera galatea*'. That these two genera might be closely related was suggested by Fry (1980b), who thought it 'possible that *Melidora* and *Tanysiptera* are of immediate common descent and the former is a specialised derivative that has retained, in the adult, the ancestral juvenile plumage'. The presence of similar plumages is also evident in female *Lacedo* and some species of *Actenoides*, notably *A. princeps* and *A. lindsayi* of all ages. This resemblance between *Actenoides* and *Tanysiptera* and between *Lacedo* and *Melidora* was commented on by Fry (1980b).

Bell (1981) also considered that *Melidora* was closest to *Tanysiptera*. He noted that the call notes of these two species were similar and the distress notes identical. They have similar skeletal proportions, particularly in the relative length of the legs when compared to *Todiramphus*, *Halcyon* or *Dacelo* (Boles, unpubl. data). These two genera thus have more similarities than might be immediately obvious. They also share habitat preferences. Although *Melidora macrorrhina* and *Tanysiptera* species will enter mangroves, teak plantations and drier adjacent country, they are primarily occupants of rainforests. *Lacedo pulchella* and the 6 species of *Actenoides* inhabit rainforest, preferably in a primary, undisturbed state.

Species of *Todiramphus* are uniform in plumage. Most have a variation of the basic pattern of green or blue upperparts and white or light orange underparts and collar. Several subgroups can be discerned, but they still show only small divergences from this general form. These species are almost all sit and pounce feeders. Habitat preferences among species are more varied, ranging from rainforest to open country. Within Australo-Papua, however, few occur in rainforest and there is a decided bias towards open forest, woodland, mangroves, clearings and open country. Most rainforest inhabiting forms are found on islands of the southwest Pacific.

The processus dentiformis in the Riversleigh kingfisher is smaller than that in primitive modern forms. This could indicate that it has been undergoing reduction since the split of its lineage from that of *Tanysiptera–Melidora*. In this respect it is consistent with what would be predicted for a primitive species of *Todiramphus*. The bone exhibits a largely *Todiramphus* character while retaining this more primitive halcyonid feature.

The identification of the Riversleigh fossil as a halcyonid is compatible with Fry's (1980a) interpretation, as is considering the presence of the processus dentiformis as primitive. According to Fry's scenario, an early Miocene kingfisher should be a primitive form. His criteria, however, are not useful in this situation. The foraging methods of the fossil cannot be determined, nor can its systematic isolation be ascertained. The Riversleigh habitat is considered (Archer et al., 1992) to have been rainforest, but this cannot be used as a character for making a taxonomic determination.

Although this fossil permits identification as a halcyonid kingfisher, it is not clear whether this species belongs to an existing genus or should be

allocated to a new one. The presence of a feature found in living primitive genera and the kingfisher's occurrence in what is considered to have been rainforest suggest that it, too, was a more primitive form. This is consistent with the sequence of evolutionary events suggested by Fry (1980a).

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